

Cave Collembola of South-East Asia

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동남아시아의 동굴산 톡토기

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적 요*

동남아시아의 열대지역 동굴에서 톡토기를 채집하기 위해 Luzon(필리핀), 파푸아 뉴기니아, Sulawesi(인도네시아), 말라야, 타이랜드에 수차 원정을 실시하였다. *Acherontiella*, *Pseudosinella*, *Sinella*, *Oncopodura*, *Arrhopalites* 등 속들이 조사지역의 모든 동굴에서 서식하고 있었다. 그러나 수개 속은 분포상 매우 제한되어 있었다. *Troglopedetes*는 동남아시아 대륙에서는 현저한 분화상을 보였으나 다른 곳에서는 볼 수 없었다. *Coecoloba*는 파푸아 뉴기니아에서만 관찰될 뿐이고 멀리 떨어져 한국과 일본지역에서 다시 나타나고 있다. 대개의 종들은 토양산 계통으로 현재까지 유존종(遺存種)으로 생각되는 것은 발견되지 않았다.

Key Words: Cave, Collembola, Southeast Asia, Taxonomy

INTRODUCTION

Few data are available about South-East Asia Collembola. Four species are recorded from Batu

*The abstract of this paper was presented at the 16th Pacific Science Congress held in Seoul during August 20-30, 1987. Its translation into Korean as above has been done by Dr. Lee, Byung-Hoon.

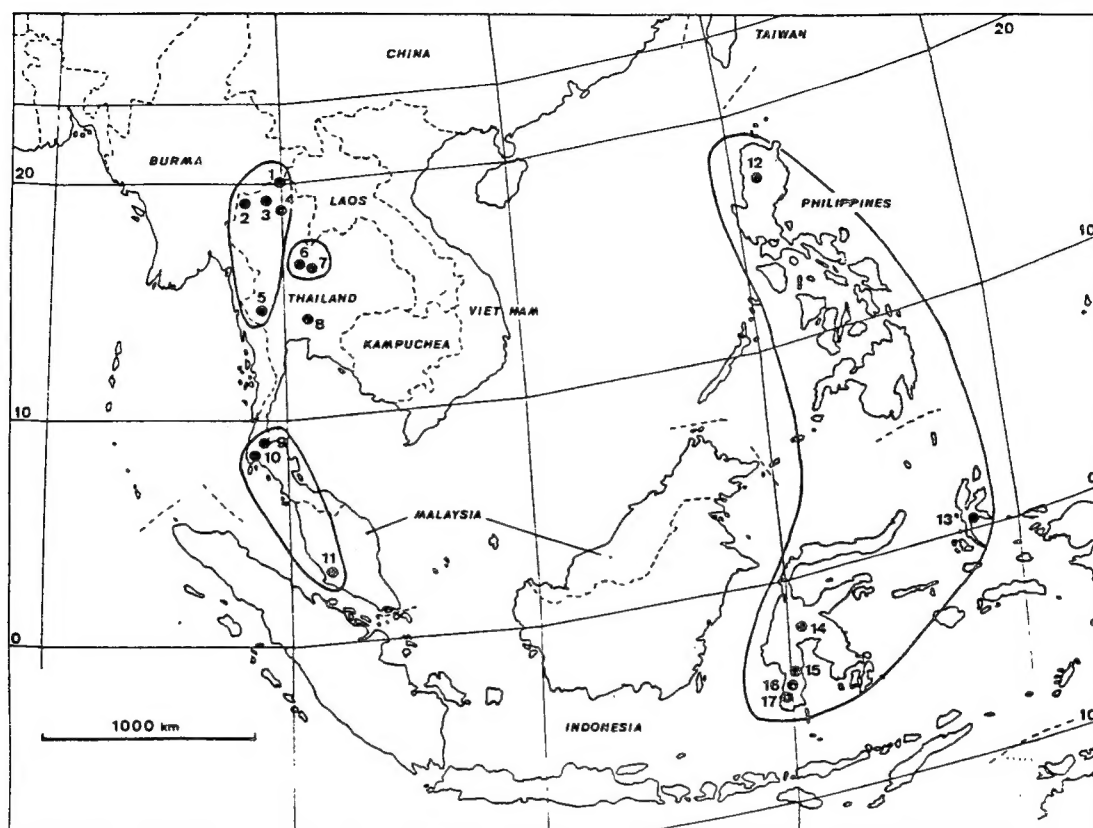


Fig. 1. Localities of the cave Collembolan fauna known in South-East Asia. 1 to 5: Western and Northern Thailand fauna with *Troglopedetes* gr. A (provinces: 1, Chiang Rai; 2, Mae Hong Son; 3, Chiang Mai; 4, Lampang; 5, Kanchanaburi). 6-7: Phetchabun and Chaiyaphum provinces (Thailand), fauna with troglomorphic *S. (Sinella)* spp. 8, Saraburi province (only one cave sampled). 9 to 11: Southern Thailand (provinces: 9, Surat Thani; 10, Phangnga) and Malaya (11, Batu caves), fauna with *Troglopedetes* gr. B. 12 to 17: fauna with *Pseudosinella* gr. A in Philippines (12, Sagada karst), Halmahera (13, Batu Lubang cave), Sulawesi (karstic areas: 14, Toradjas; 15, Watampone; 16, Malawa; 17, Maros).

caves (Malaysia) by MacLure *et al.* (1967) and Carpenter (1933). All other observations come from French expeditions to Philippines (1979), Indonesia (1985 and 1986) and Thailand (1981, 1985, 1986 and 1987) (Deharveng *et al.*, 1986; Deharveng, 1986 and 1987). The investigated areas are illustrated on Fig. 1. Information is completely lacking for the huge karsts of South China and Indochina, the islands of Sumatra, Java, Borneo, lesser Sunda, most of the Philippines and of the Moluccas. In neighbouring regions, a few cave Collembola are known from New Guinea, Burma and India.

As a large majority of the cave species collected are not yet described, this paper aims to give only a very preliminary account of the Collembolan fauna of South-East Asia.

1. Lines and species of Collembola from South-East Asia caves

1-1. Cave-restricted species

The cave-restricted Collembola collected in South-East Asia belong to 8 major lines; each line is represented by several species with large populations in most caves of its range. In addition, a few

rare or poorly known species occur locally. All but 2 species are new to science.

1-1-1. *Acherontiella*: two non-troglophilic species of this genus are present in northern Thailand caves (Table 4); they were extracted from guano and from clay around roots. In this area, we failed to find any *Acherontiella* in soil, but edaphic forms are present in South Sulawesi. Likewise, the species of Europe or America are either edaphic or cavernicolous.

1-1-2. *Willemia*: species have been found in Southern Thailand (tham Pong Chang, on guano), Malaya (*W. nadchatrami* in Batu caves, unknown habitat) and South Sulawesi (gua Salukkan Kallang, in flood debris). In these regions, no species of the genus has been collected in the soil which is the habitat of all the other known species of the genus in the world. *Willemia* are edaphophilic in morphology.

1-1-3. *Troglopedetes* group A (Fig. 2): this line is characterized by a fourth antennal article subdivided in two parts and a distinct pattern of dorsal macrochaetae. It groups several closely related species frequent in soil and caves of Northern and Western Thailand. Their morphology vary from nontroglophilic in edaphic species to highly troglomorphic in the most evolved cave species.

1-1-4. *Troglopedetes* group B: this group is characterized by an entire fourth antennal article and a very reduced dorsal macrochaetae pattern. It includes at least 3 troglomorphic species from Southern Thailand. Related forms are present in the soil of the same area. The affinities of this line inside *Troglopedetes* are not clear.

1-1-5. *Pseudoparonella doveri* probably belongs to the genus *Troglopedetes* (gr. C); this peculiar species from Batu caves (Malaysia) has no epigeic relatives.

1-1-6. *Sinella* (*Coecobrya*) gr. *caeca*: the subgenus *Coecobrya* is distinct from *Sinella* by its smooth spiny setae on the dorsal side of dens and manubrium; the absence of eyes and pigment, the short antennae (<2, 5 times the cephalic diagonal) and the falciform mucro are characteristic of the *caeca* group. Species are widespread in South-East Asia soil and caves (often on guano), but none was collected in Sulawesi and Halmahera. Morphology is not or slightly troglomorphic.

1-1-7. *Sinella* (*Sinella*) spp.: a group of troglomorphic cave-restricted species inhabit caves of Phetchabun and Chaiyaphum provinces in Thailand. They display the ordinary characters of the subgenus *Sinella* (no smooth spiny dorsal setae on dens and manubrium); in addition, they have no eyes, no pigment and they differ from other species described hitherto by their very long antennae (>3, 5 times the cephalic diagonal) and their falciform mucro. No species of this group was found in the soils of the regions prospected in South-East Asia.

1-1-8. *Pseudosinella* group A: this group is characterized by the presence of a few smooth spiny setae on the dorsal side of dens and manubrium. It includes several blind species from soils and caves of Philippines, Sulawesi and Halmahera; cavernicolous forms are troglomorphic. The world distribution of this line is not known, but it is present at least in New Guinea (undescribed cave species).

1-1-9. *Oncopodura* gr. *tricuspidata*: a few troglomorphic specimens were collected in 2 caves of Northern Thailand; no species was obtained from soil samples.

1-1-10. Other cave-restricted species were collected in one locality only; they appear on the table 1 to 4.

1-2. Non cave-restricted species

1-2-1. *Arrhopalites* spp. were collected in several caves of Northern Thailand and Sulawesi. They have not been studied in details, but some of them at least could be different from their epigeic relatives of the same regions.

Table 1. Collembola collected in the Sagada karst caves (Philippines: Luzon island) (unpublished data)

Species	Usual habitat in the area
Neanuridae	
<i>Vitronura</i> sp.	soil
Onychiuridae	
<i>Protaphorura</i> spp. (2 sp.)	guano?
<i>Mesaphorura</i> sp.	soil
Isotomidae	
<i>Folsomia candida</i> Willem, 1902	cave, soil
<i>Folsomia</i> , sp.	soil ?
<i>Folsomides exiguus</i> Folsom, 1932	soil, cave
<i>Folsomina onychiurina</i> Denis, 1931	soil, cave
<i>Isotoma</i> sp.	soil
<i>Isotomiella</i> sp.	soil
Entomobryidae	
<i>Acrocyrus</i> sp.	soil
<i>Ascocyrtus</i> spp. (2 sp.)	soil
<i>Lepidocyrtus</i> sp.	soil
<i>Pseudosinella</i> line A sp.	cave, soil ?
<i>Sinella</i> (<i>Caecobrya</i>) gr. <i>caeca</i> (Schött, 1896) sp.	cave: guano
Paronellidae	
<i>Bromacanthus</i> spp. (2 sp.)	soil

1-2-2. Regular trophophilic species *Folsomides exiguus*, *Folsomina onychiurina* and *Isotomiella* sp. are present in many caves of South-East Asia; these forms usually live in the soils of the whole tropical Asia. In Sagada (Philippines), the parthenogenetic *Folsomia candida* is frequent in caves and soil, like in temperate Europe.

1-2-3. A number of accidental species are found in South-East Asia caves, particularly when the underground systems are in relation to the surface through river sinks. Collembola are swept down by the flood during rainy season and some can survive in organic debris on the banks of the subterranean streams. Tables 1 and 2 give lists of such accidental Collembola collected in the Sagada and Sulawesi caves.

2. Main types of regional fauna

(Fig. 1)

On the basis of the data exposed above, cave fauna of South-East Asia appears rather heterogeneous. One line-*Sinella* (*Caecobrya*) gr. *caeca*-is present in all regions except Sulawesi and Halmahera, probably with different but very closely related species. The other lines have more restricted distributions and lead us to recognize different regional fauna.

Pseudosinella gr. A is the only group which gave troglobite non-guanobiont species in Sulawesi and Halmahera. Some guanobiont species have also been collected in this area (*S. (Caecobrya)* gr. *caeca*

in Sagada, and a microphthalmic *S. (Caecobrya)* sp. in Mampu cave, Sulwasi).

The cave fauna is more diversified in continental karsts with three main regional types characterized by original lines.

In Malaya (Batu caves) and southern Thailand (Phangnga, Surat Thani), *Troglopedetes* gr. B and

Table 2. Collembola collected in Sulawesi and Halmahera caves.

Species	Stations	Usual habitat in the area
Hypogastruridae		
<i>Willemia</i> sp.	M	soil ? or cave
Brachystomellidae		
<i>Brachystomella</i> sp.	M	soil
Neanuridae		
<i>Blasconura</i> sp.	M	soil
<i>Friesea</i> sp.	M	soil ?
cf. <i>Lobella</i> sp.	M	soil
cf. <i>Micranurida</i> sp.	M	soil ?
<i>Paleonura</i> sp.	M	soil
<i>Paranura</i> sp.	M	soil
cf. <i>Pseudachorutella</i> sp.	M	soil ?
Onychiuridae		
<i>Mesaphorura</i> sp.	M,W	soil
Isotomidae		
cf. <i>Denisia</i> sp.	M	soil
<i>Folsomides exiguus</i>	M	soil, cave
<i>Folsomides</i> sp.	M,W	soil
<i>Folsomina</i> sp.	W	soil, cave
<i>Isotomiella</i> sp.	M,W	soil, (cave)
Oncopoduridae		
<i>Harlomillsia</i> sp.	A,W	soil, (cave)
Entomobryidae		
<i>Lepidocyrtus</i> sp.	W	soil
<i>Pseudosinella</i> group A (2-3 sp.)	M,W,A,H	cave
cf. <i>Pseudosinella</i> sp.	M,W	soil, cave
Oculated <i>Sinella (Caecobrya)</i> sp.	W	cave (guano)
Arrhopalitidae		
<i>Arrhopalites</i> sp.	W,T	soil ? or cave
Neelidae		
<i>Megalothorax</i> sp.	M,W	soil

M: caves of the Maros karst; W: gua Mampu in the Watampone karst; A: gua Mangana in the Malawa karst; T: gua Londa in the Toradja karst; H: Batu Lubang cave on Halmahera (Deharveng, 1987 and unpublished data)

Table 3. Collembola of Batu caves (Malaya) (Carpenter, 1933; MacLure *et al.*, 1967)

Hypogastruridae	<i>Willemia nadchatrami</i> Yosii, 1959
Brachystomellidae	<i>Brachystomella contorta</i> Denis, 1931
Entomobryidae	<i>Sinella (Caecobrya) gr. caeca</i> (Schött, 1896)
Paronellidae	<i>Pseudoparonella doveri</i> Carpenter, 1933

Care regular troglobites while *S. (Caecobrya) gr. caeca* and *Willemia* spp. frequently occur in the guano.

In Western and Northern Thailand (Chiang Mai, Chiang Rai, Kanchanaburi, Lampang, Mae Hong Son), troglobites are represented by several *Troglopedetes* gr. A species, and locally by *Pseudosinella* sp. or *Oncopodura* sp. (Table 4). In the guano, *Acherontiella* spp. are sometimes present, while *S. (Caecobrya) gr. caeca* is more frequent.

Phetchabun and Chaiyaphum caves shield an original troglomorphic line of *S. (Sinella)*; *S. (Caecobrya) gr. caeca* are again present in number on the guano, but we failed to find any *Troglopedetes* there.

3. Evolution and speciation in tropics: general information brought by the study of South-East Asia cave Collembola

3-1. Morphological evolution of cave Collembola

South-East Asia Collembola have given a lot of troglomorphic species in the genera *Troglopedetes*, *Pseudosinella*, *Sinella* and *Oncopodura*. They occur at any altitude, but troglomorphy is often stronger in colder caves. Nearly all non-guanobiont troglobites are even troglomorphic in our material. The cave adaptations are the same as those well-known under temperate climates: loss of the eyes and pigment, elongation of legs and antennae, thinner and simpler claw, larger body size (Fig. 2). Similar evolutions are observed in cave *Troglopedetes* of tropical America (Palacios-Vargas *et al.*, 1985). The opinion expressed by Vandel that tropical cave were devoid of morphologically cave-adapted troglobites can no longer be supported for Collembola. It is even clear that in South-East Asia the number of troglomorphic species and the degree of troglomorphy are as high as in many temperate countries.

It comes that the selective pressure leading to troglomorphic morphology can operate under temperate or tropical climate: they are at least for a part independent of the regional climatic and paleoclimatic conditions and mostly linked to characters of the subterranean habitat shared by tropical and temperate caves.

3-2. Relictual and non-relictual lines

A sufficient knowledge of both cavernicolous and epigeic Collembolan fauna in a given area as well as precise phylogenetic information are necessary to establish the relictual or non-relictual character of a line. Such conditions are seldom fulfilled for South-East Asia Collembola, but a few lines can be analysed in this scope: *Troglopedetes* gr. A, *Pseudosinella* gr. A, *Sinella (Caecobrya) gr. caeca* and *Oncopodura gr. tricuspidata*.

Among them, *Oncopodura gr. tricuspidata* is the only probable relictual line. It includes two rare cave species of Northern Thailand, a region which has been extensively sampled for edaphic fauna:

no species of this group has ever been found in the soil there, and the geographically nearest species was reported from soil in India (*O. indica*). Several cave species are present in Europe where they also appear to be relictual.

Troglopedetes gr. A has a number of closely related species from caves and soils of Northern and Western Thailand; they show a nice morphological cline linked with the habitat of the species. It runs from soil species of small size which possess eyes, pigment, fairly short appendages and thick claw with several large teeth, to highly troglomorphic cave-restricted species of large size which have no eyes, no pigment, long appendages and thin claw with small basal teeth (Fig. 2).

Similar cline occurs in *Pseudosinella* gr. A in Sulawesi. At last, *S. (Coecobrya) gr. caeca* has closely related forms in caves and soils of Sulawesi and provides a third example of non-relictual cave species.

On the whole and in spite of the lack of data for several lines, the cave Collembola of Thailand comprise at least a large proportion of non-relictual species. The non-relictual character of certain cave fauna, established by Howarth (1981) for Hawaii, is thus met again in Thailand where the caves

Table 4. Cave restricted Collembola of Thailand (Deharverg, 1986 and unpublished data)

Species	Province (caves)
Hypogastruridae	
<i>Acherontiella</i> (>2 sp.)	Chiang Mai (Klaeb Yai, Tab Tao) Lampang (Pha Thai)
<i>Willemia</i> sp.	Phangnga (Poung Chang)
Onychiuridae	
<i>Protaphorura</i> sp.	Chiang Mai (Chiang Dao)
Isotomidae	
<i>Folsomia</i> sp.	Chiang Rai (Khu Khan)
Oncopoduridae	
<i>Oncopodura</i> gr. <i>tricuspidata</i> (2 sp.)	Chiang Mai (Klaeb Yai) Mae Hong Son (Pha Mon)
Entomobryidae	
<i>Pseudosinella</i> sp.	Chiang Mai (Chiang Dao)
<i>Sinella (Coecobrya) gr. caeca</i> (>2 sp.)	most caves
<i>Sinella (Sinella)</i> (2-3 sp.)	Chaiyaphum (Phulu, Ngoem) Phetchabun (Sombat)
Oculated <i>S. (Sinella)</i> sp.	Saraburi (Thap Kwang)
Paronellidae	
<i>Troglopedetes</i> group A (>5 sp.)	many caves in Chiang Mai, Chiang Rai, Kanchanaburi, Lampang, Mae Hong Son
<i>Troglopedetes</i> group B (3 sp.)	Phangnga (Poung Chang) Surat Thani (Tha Chana)
Arrhopalitidae	
<i>Arrhopalites</i> (2 sp.)	Chiang Mai (Chiang Dao, Klaeb Yai) Chiang Rai (Khu Khan)

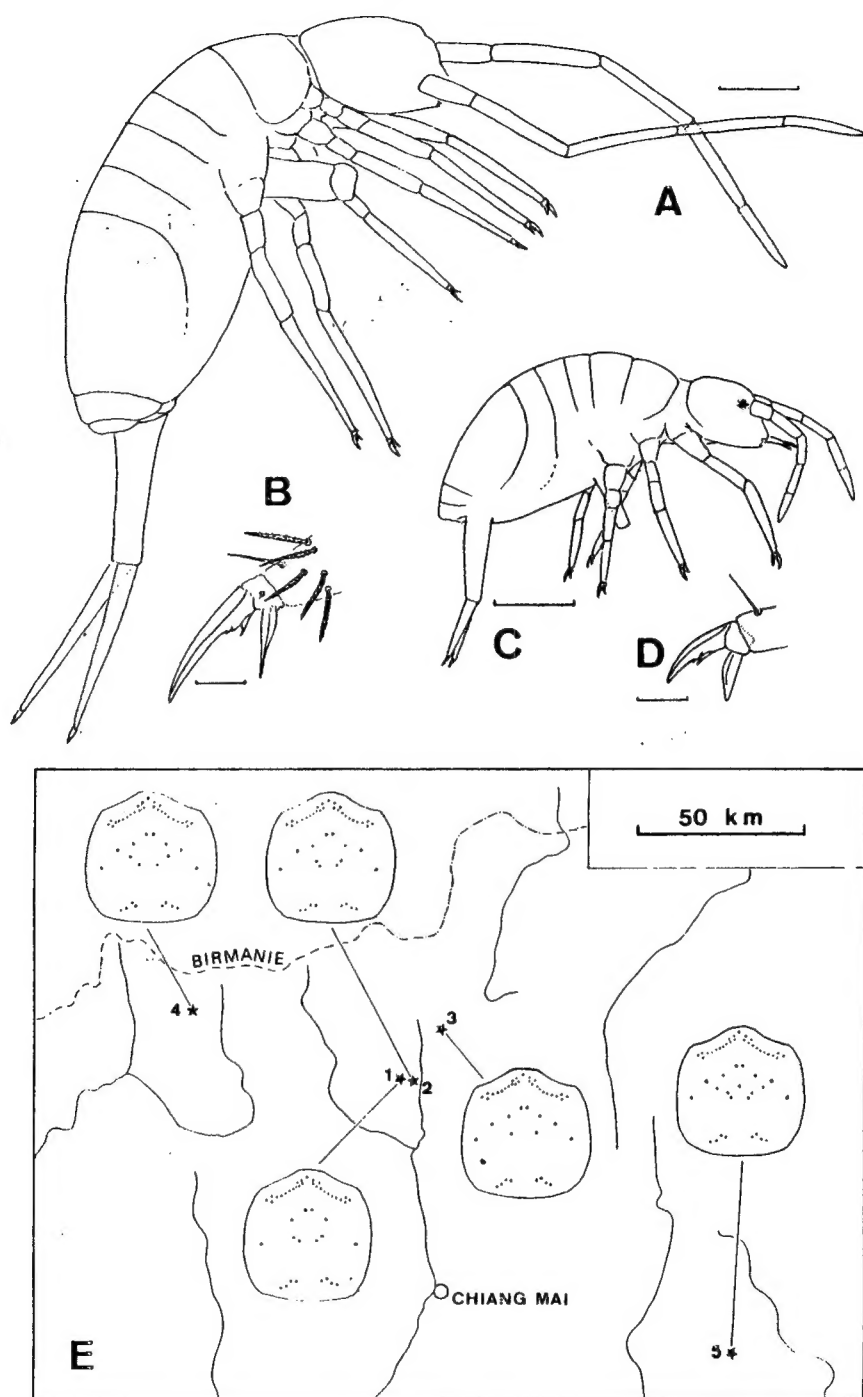


Fig. 2. A,B: cave *Troglopedetes* sp. (gr. A) from tham Pha Mon (Mae Hong Son), habitus (A) and claw III (B); C,D: soil *Troglopedetes* sp. (gr. A) from the same area, habitus (C) and claw III (D); E: some cave *Troglopedetes* sp. (gr. A) from Chiang Mai and Mae Hong Son provinces in NW Thailand with their characteristic cephalic pattern of macrochaetae. 1, tham Chiang Dao; 2, tham Ban Oui Haen; 3, tham Klaeb Yai; 4, tham Pha Mon; 5, tham Pha Thai. Tham = cave in Thai language. Scales: A, C: 200 μ m; B, D: 10 μ m.

are much older and the fauna more complex.

3-3. Endemism

Very little is known about endemism and speciation in tropical caves. We can present here some preliminary results concerning the cave restricted species of the genus *Troglopedetes* in Northern Thailand (Deharveng, 1986 and Fig. 2). Evolution has operated on presumed non-adaptative characters of the dorsal macrochaetotaxy and adaptative characters linked to the underground habitat (as listed above). Microgeographic differentiation of the populations seems to be the rule. Each karstic unit has its own species of *Troglopedetes* which differs slightly from that (or those) of the nearest karstic unit. Apparently, gene flow cannot easily escape the limits of the limestone. In temperate countries, superficial underground compartment (SUC) in non limestone rocks is the way used by many troglobites to spread beyond these limits: populations of different karstic units can thus be genetically linked together thanks to SUC (Juberthie, 1983). Under humid tropics, SUC is probably absent or poorly developed because of the paleoclimatic and climatic conditions (no glaciations, and filling up of cracks and boulders); the resulting parcelling of the subterranean habitat would be therefore more accentuated and each karstic unit more isolated: this situation could account for the high level of endemism observed in cave *Troglopedetes* of Northern Thailand.

Such an hypothesis has, however, to be checked on other terrestrial groups of cave-dwelling animals.

Conclusions and perspectives

The intensive researches about South-East Asia cave Collembola began just a few years ago. A huge basic work of material collection and taxonomic studies have to be carried out first. However, the data based on generic or species-group identifications are already sufficient to draw out some general considerations and hypothesis which fit to new trends in tropical biospeleology. They can be summarized as follows:

- (1) South-East Asia caves shield a true troglobiont fauna of Collembola.
- (2) The troglobites are morphologically cave-adapted in the same way as temperate troglobites.
- (3) At least a large part of them are non-relictual forms related to actual epigeic species of the same region.
- (4) The fauna is far from uniformity and several faunistic regions can already be recognized on the few available data.
- (5) A high level of endemism has been observed in the only line studied in details, but could well be the rule among the cave-restricted Collembola if it is linked to a particular structure of the underground compartment in the tropics.

ABSTRACT

Several expeditions have recently been undertaken for collecting Collembola in tropical caves of south-east Asia, where its fauna was virtually unknown. Data are now available for Luzon (Philippines), Papua New Guinea, Sulawesi (Indonesia), Malaya and Thailand. This cave fauna shows a large stock of genera shared by most of the prospected areas and the temperate caves: *Acherontiella*, *Pseudosinella*, *Sinella*, *Oncopodura* and *Arrhopalites*. However, a few genera are more restricted in distribution. *Troglopedetes*

is well differentiated in the continental south-east Asia, but absent in other part of the region, whereas *Coecoloba* is only known from Papua New Guinea, and occur again in the Coreo-japanese area. Most species belong to lineages present in the soil, and no relictual form has been discovered until now.

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RECEIVED: 1 SEPTEMBER, 1987

ACCEPTED: 30 OCTOBER, 1987